

**BEHAVIOR AND DEVELOPMENT OF THE WASP  
*PTEROMBRUS RUFIVENTRIS HYALINATUS* KROMBEIN  
(HYMENOPTERA: TIPHIIDAE), A PARASITE OF LARVAL  
TIGER BEETLES (COLEOPTERA: CICINDELIDAE)**

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*Abstract.*—*Pterombrus rufiventris hyalinatus* was found attacking third instar larvae of three *Cicindela* species in Arizona. Its parasitic behavior is generally similar to that described for tropical species of *Pterombrus*, but different in having a more elaborate burrow plugging behavior and one generation per year. Female wasps enter open burrows or occasionally dig into plugged burrows, sting the host larvae several times under the head or thorax, and oviposit on the second abdominal sternum. Burrows are closed with a primary plug of compacted soil immediately above the larvae and a secondary plug loosely packing the remainder of the burrow. Mean development time is 2.93 days for the egg stage and 8.70 days for larvae. When mature, wasp larvae detach from the host, spin a cocoon in the larval burrow, and emerge the following July with the onset of the "monsoon" rains.

*Key Words:* *Cicindela*, larvae, parasite, parasitic behavior, *Pterombrus*, tiger beetle, Tiphiidae, wasp

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Two genera of tephritid wasps of the subfamily Methochinae, *Methocha* and *Pterombrus*, are parasites of tiger beetle larvae. Some of the natural history and behavior of several species of *Methocha* has been described (Adlerz 1906, Williams 1916, 1919, Iwata 1934, 1936, Burdick and Wasbauer 1959, Wilson and Farish 1973). *Pterombrus* is primarily tropical in distribution and the limited knowledge about it comes from studies of *P. cicindeloides* and *P. iheringi* in Brazil (Williams 1928) and *P. piceus* in Costa Rica (Palmer 1976). These studies included field observations and notes of parasitic behavior and development times.

*Pterombrus rufiventris* is the only known

United States species of the genus. Krombein (1949) distinguished two subspecies, *P. r. rufiventris* from eastern Texas, Louisiana, North Carolina, and Virginia, and *P. r. hyalinatus* from western Texas, Arizona, and California. Nothing has been published on the biology of this species. During ecological studies of tiger beetles in southeastern Arizona, one of us (CBK) discovered *P. r. hyalinatus* parasitizing larvae of *Cicindela obsoleta*, *C. pulchra*, and *C. marutha*. Because of its possible importance in limiting these tiger beetle populations, field and laboratory studies of this wasp were initiated. We present here observations on parasitic behavior and development. Other studies present rates of parasitism of *Cicindela*

species (Knisley 1987, Knisley and Juliano, 1988) and factors that influence rates of parasitism (Knisley, in prep.).

#### METHODS

**Field studies.**—Field studies were done in the Sulphur Springs Valley, near Willcox, Cochise Co., AZ, during July and August from 1983–87. Eight sites representing four habitat types (playa, saltbush flat, grassland, sand ridge), each with one or more species of adult or larval *Cicindela* (Knisley 1987) were checked for wasps one to two times per week. During these checks all *Pterombrus* were counted to determine relative abundance and seasonal activity. Wasp behavior was observed and recorded.

**Laboratory studies.**—The behavior of *Pterombrus* was studied under laboratory conditions of summer photoperiod (13L:11D) at 24–28°C in an observation chamber. The chamber was made from a transparent plastic “shoe” box (17 × 32 × 9 cm) and supported by 20 cm wooden legs placed under each corner. An acrylic tube (2.5 × 18 cm) filled with soil and containing an active third instar of *C. pulchra* (Knisley and Pearson 1984) was inserted through a hole in the bottom of the box so that the top of the tube was flush with the surface of a 5–6 cm layer of soil in the box. The top of the tube was wrapped with tape to ensure a tight fit of the tube into the hole. For clear observation of wasp behavior, only tubes in which the larva had dug a burrow along the side wall of the tube were used for the trials. To begin an observation trial a female wasp was placed into the covered plastic box. We observed the complete sequence of parasitic behavior for three wasps and partial sequences for three others.

Development time of *Pterombrus* was determined from host preference studies (Knisley, in prep.) in trials in which a tiger beetle larva in a rearing tube was confined with a wasp. Each parasitized larva was carefully dug from the tubes and transferred onto a disc of moistened paper towel in a

plastic petri dish (10 cm dia). Developmental progress and body length of larval stages were recorded daily.

#### RESULTS AND DISCUSSION

**Field studies.**—Distribution and behavior of wasps in the field were based on over 70 sightings of adult wasps. Only four males were observed and all were flying near females and appeared to be attempting to mate. No mating was seen. Adult wasps were found at six sites. Only one wasp was observed each at two of these sites, a ditch edge and a pond edge. No wasps were observed in the playa or playa edge habitats. Wasps were relatively common (two to five observed during each survey) at two sand ridge sites where there were large populations (over 500) of *C. marutha* larvae and at a nearby (400 m) saltbush flat where there were several hundred *C. pulchra*. *Pterombrus* was also common at a higher elevation grassland site near Chiricahua National Monument which had a population of over 300 *C. obsoleta* larvae.

Adult wasps were first observed at field sites within one or two days of the first significant July rainfall (>8–10 mm). The actual dates of first sightings were July 6 in 1986, July 10 in 1985 and July 16 in 1987. Wasp emergence may be triggered by the onset of the summer “monsoon” rains, as is tiger beetle adult emergence and larval activity. Numbers of wasp sightings decreased from July through late August at all sites, but the pattern of abundance at the grassland site was about two weeks later than at the other sites. In the field, we observed *P. r. hyalinatus* parasitizing only third instars of *C. pulchra*, *C. obsoleta*, and *C. marutha*, but in the laboratory some second instars of these species were attacked. Palmer (1976) found that *P. piceus* parasitizes primarily second instars of *Pseudoxychila tarsalis* Bates.

**Searching behavior.**—We observed the searching behavior of 15 wasps in the field. Female wasps walked rapidly over the

ground, frequently turning and darting, in what appears to be a random pattern. The wasps stopped to examine or probe with their antennae holes, cracks or surface depressions. Often they passed within several centimeters of active larval burrows then moved away. Wasps initiated an attack only when they came in contact with the burrow edge. *Pterombrus piceus* searches in a similar manner and seems to prefer to attack larvae that move down the burrow when they approach (Palmer 1976).

We observed four instances of wasps digging out plugged burrows of third instar *C. marutha*, a species which typically plugs its burrows during most of the day (Knisley 1987). In each case, the wasp used its mandibles to grasp bits of sand from the plugged area, moved back 4 to 6 centimeters and dropped the sand, eventually forming a small arc or circle of sand around the burrow mouth. Removal of the 2 to 4 cm plug took 19 to 33 minutes, after which the wasp entered the burrow to attack the larva. *Methocha* (Padgen 1926) and *P. iheringi* (Williams 1928) have also been observed digging out plugged burrows. In addition, *Methocha* reportedly digs in soil where tiger beetle larvae had previously occurred (Williams 1919). These observations suggest that wasps may detect the odor of host larvae or their burrows once they come in close proximity to them. In the laboratory chambers, *Pterombrus* initiated attacks on larvae in 4 to 38 minutes ( $\bar{x} = 16.2$ ). In the field, wasps were observed to search for 15–30 minutes without finding a larva.

*Pterombrus* did not seem to fly when searching for burrows, and seldom flew unless disturbed. Short flights (7–20 m), observed when wasps searched unsuccessfully in an area for 15 to 20 minutes, could indicate dispersal to new areas of potential larval habitat.

Attack, stinging and oviposition.—Attacks of host larvae in the laboratory were initiated by female *P. r. hyalinatus* moving quickly into the burrow head first, causing

the larva to retreat. The wasp continued down the burrow until her head touched the larva's head. Sometimes the wasp used its mandibles to grasp the head of the larva before quickly curving her abdomen forward and stinging the larva under the head or thorax. This caused the larva to move further down the burrow. The wasp remained inactive for 2–5 minutes, then cautiously approached the larva and probed the larva's head with its antenna. In two of the trials with large third instars of *C. obsoleta*, the larvae responded with slight movement and were again stung once or twice.

The wasp used one or more of three methods to slightly raise the larva in the burrow: grasping the larva's head with its mandibles and pulling from above, pushing up on the caudal portion of the larva's abdomen, or grasping the larva's forelegs with its mandibles and pushing while positioned beside the larva. These movements often wedged the larva's cephalothoracic shield in the burrow. In two cases another sting was then applied to the larva's venter. We never observed larvae flipping out of the burrow. This may be a defense reaction of the larva and is reported in studies of *Pterombrus* (Palmer 1976) and *Methocha* (Mury Meyer 1983). We also did not observe wasps being seized by tiger beetle larvae. *Methocha* has been observed to allow the larva to seize it with its mandibles before quickly stinging the larva. Palmer (1976) reported one instance of this behavior in *P. piceus*.

After positioning the larva or sometimes after oviposition the wasp used the tip of its abdomen to pack the bottom of the burrow. *Pterombrus iheringi* shows similar packing behavior after using its mandibles to loosen the soil (Williams 1928). We observed one wasp grasp at the larva's second abdominal sternum. The wasp may have been chewing, feeding or preparing an oviposition site. Burdick and Wasbauer (1959) reported that *M. californica* commonly feeds on fluids exuding from sting punctures and suggested that this may provide nutrients



that are necessary for successful oviposition.

To oviposit, the wasp positioned itself venter to venter with the larva, moved forward using the tip of its abdomen to sweep back and forth over the larva's abdominal sternites, then stopped and deposited an egg on the midline of the second abdominal sternum. In two cases the wasp next stung the beetle larva one or more times near the egg. These stings or the chewings near the oviposition site may prepare an access for the newly hatched wasp larva to enter the host to feed.

The number of stings given the beetle larva by both *Pterombrus* and *Methocha* is variable. Any movement by the larva seems to be sufficient to trigger a stinging response in *Methocha* (Burdick and Wasbauer 1959). Our observations suggested this may be true for *Pterombrus*. Stings also seemed to be given after certain behavioral events, such as positioning the larva and oviposition. Host larvae were apparently completely paralyzed by the stings because they did not move in their burrows, and exhibited only slight movement when probed. The effect of the stings of *Methocha* species has been correlated with the site of oviposition. Host larvae stung by species that oviposit on the host's abdomen are permanently paralyzed by the host; host larvae stung by species that oviposit on the venter of the metathorax recover and move actively in their burrows (Williams 1919, Iwata 1936).

Burrow preparation and plugging.—After oviposition the wasp moved above the larva and constructed two plugs, a compact primary plug immediately above the larva and a loosely packed secondary plug which filled the rest of the burrow. To form the primary plug, the wasp positioned itself 2–4 cm above the paralyzed larva, curved its abdomen forward across the burrow shaft and used its mandibles to dislodge soil particles from the sides of the burrow. Soil fell onto the underside of the abdomen, was compacted there with the hind legs and then pressed

onto the sides of the burrow with the abdomen. As the wasp moved in a circle, the activity eventually formed a circular shelf of soil. To complete the primary plug, the wasp moved to near the top of the burrow, used its mandibles to dislodge soil onto the shelf, then moved down and appeared to use its hind legs to cover the hole in the shelf left by its abdomen. The primary plug was 1.5–3.0 cm thick and required 7–15 minutes to complete.

Next, the wasp left the burrow and searched the area within 10–20 cm of the burrow entrance for bits of soil, stones, twigs and other materials for the secondary plug. The wasp carried each piece in its mandibles and usually dropped it into the burrow from without. Filling of the burrow and completion of the secondary plug required from 21 to over 140 trips and 13–41 minutes ( $\bar{x}$  = 18,  $n$  = 12). Types of materials available around the burrow and depth of the burrow seemed to account for the variation in number of trips and time. For example, filling of burrows at the saltbush flat site required more time because plugging materials were scarce. At a sand ridge site and in two laboratory chambers where the soil was nearly pure sand, wasps formed most of the secondary plug by pushing sand into the burrow with the hind legs. Plugging was then completed by filling in with larger materials. In general, wasps seemed to be more selective of materials during the final phase of burrow plugging.

The surface appearance of the plugged burrows was distinctive at each of the sites. The secondary plugs at the grassland site consisted of small pebbles. Those at the saltbush flat had small twigs, bits of plant material or flakes of soil. Sand ridge burrows were filled with sand and often eroded around the edge. *Methocha* plugged burrows with a variety of materials (Bouwman 1909, Champion and Champion 1914), possibly selecting them on the basis of availability and ease of transport (Burdick and Wasbauer 1959). Complete closure of the

Table 1. Duration and size (length in mm) of developmental stages of *P. r. hyalinatus* reared in the laboratory at 24–28°C.

	N	Mean	SD	Range
Egg length (mm)	15	2.39	0.14	2.10–2.52
Duration egg stage (days)	14	2.93	0.59	2.30–3.90
Larval length (mm) on day after hatch:	9	2.86	0.38	2.52–3.57
2	8	3.61	0.34	2.45–4.34
3	9	4.70	0.58	3.90–6.09
4	7	6.56	0.95	5.18–7.42
5	11	5.76	1.01	4.64–6.24
6	6	9.12	1.35	5.76–10.88
7	8	9.04	2.26	8.00–11.20
8	8	14.88	1.29	13.12–16.16
Duration of larval stage (to detachment from host) (days)	15	8.70	1.35	7.80–10.50
Total development time (days)	25	12.33	2.65	10.70–15.30

burrow may be necessary to protect the developing wasp against natural enemies. We noticed that several incompletely plugged burrows were dug into by ants and the host larvae were eaten.

Plugging burrows with two plugs by *P. r. hyalinatus* involves more elaborate behavior than the single plugging by other species of *Pterombrus*. This may be an adaptation to the dry environment of *P. r. hyalinatus* where infrequent rains are less likely to naturally close the burrow. The single plug constructed by *P. piceus* (Palmer 1976) resembles the secondary plug described here. The single plug of *P. iheringi* (Williams 1928) is similar to the primary plug of *P. r. hyalinatus*. Observations of *Methocha* indicate plugging involves a complete filling of the burrow (Alderz 1906, Bouwman 1909, Burdick and Wasbauer 1959).

Development.—Upon hatching the wasp larva typically remained at the site of oviposition on the second abdominal sternum and began extracting the liquid contents of the host larva. Growth was rapid with larvae increasing by about 1–1.5 mm per day, from a mean length of 2.8 mm at hatching to 14.8 mm when fully grown after eight days. Detachment from the host and initiation of cocoon spinning began when the host was completely consumed and shriveled. The cephalothoracic shield of the host

was typically attached to the top of the pupal cocoon and apparently served as a starting point for cocoon spinning. The pupal cocoon was similar to *P. cicindelidicus* (Williams 1928). Adult *Pterombrus* collected at the saltbush flat and grassland sites which had larger host tiger beetle larvae (*C. pulchra* and *C. obsoleta*, respectively) had a mean length of 13.5 mm and those collected at the sand ridge sites with the smaller *C. marutha* had a mean length of 10.5 mm. In laboratory host preference studies pupal size was highly correlated with host larva size (Knisley, in prep.).

Mean time from oviposition to completion of the pupal cocoon was 13.2 days (SD = 1.6, range 10.2–17.3) (Table 1). Mean duration of stages was 2.93 days for the egg, 8.70 days for the larva, and 1.60 days from larval detachment to completion of the cocoon. Larval development is about 12 days for *P. piceus* (Palmer 1976) and 10–12 days for several *Methocha* species.

The behavior we observed for *P. r. hyalinatus* was similar in most aspects to that of other species of the genus. The more elaborate plugging behavior and the one generation per year may be adaptations to a different environment. Our observations also indicate similarity between the behavior of *Pterombrus* and *Methocha* and suggest that these behaviors have evolved in

response to the highly specialized life of larval tiger beetles. The apparent consistent difference between these genera is the initial attack behavior in which *Methocha* allows itself to be seized by the larva. Studies on searching, host selection, and abundance of these two genera of parasitic wasps could provide important additional information for determining how they limit tiger beetle populations.

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